

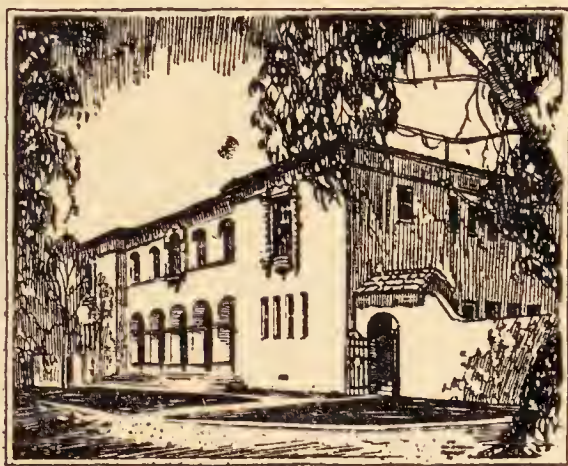
BULLETINS
OF THE
Zoological Society of San Diego

No. 15

**A Further Study of
Pattern Dimorphism in the
California King Snake**

By L. M. KLAUBER

Consulting Curator of Reptiles, Zoological Society of San Diego



SAN DIEGO, CALIFORNIA

SEPTEMBER 29, 1939



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A FURTHER STUDY OF PATTERN DIMORPHISM
IN THE CALIFORNIA KING SNAKE

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SAN DIEGO, CALIFORNIA

September 29, 1939

STANDARD PATTERNS



Fig. 1. RINGED PHASE

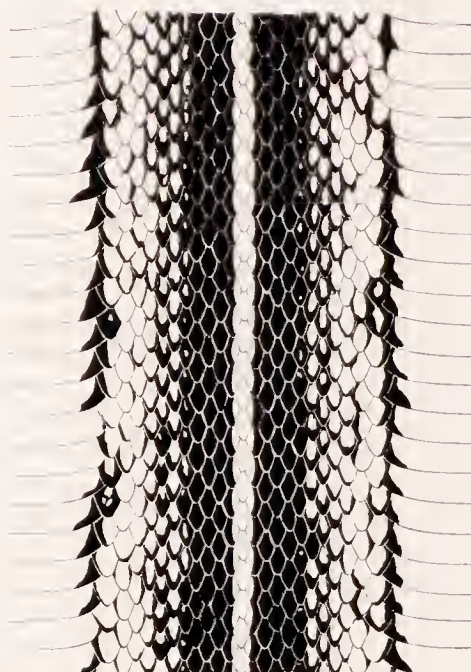


Fig. 2. STRIPED PHASE

ABERRANT PATTERNS

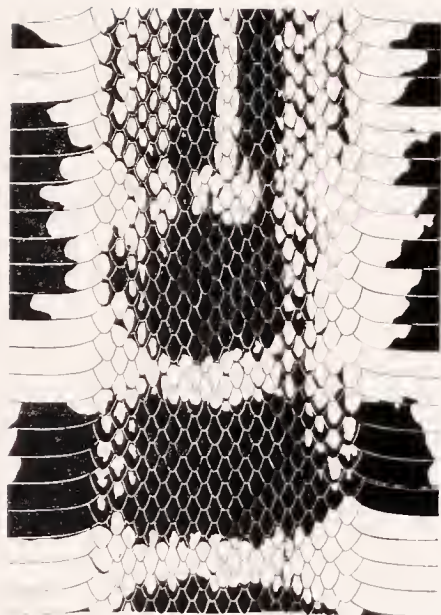
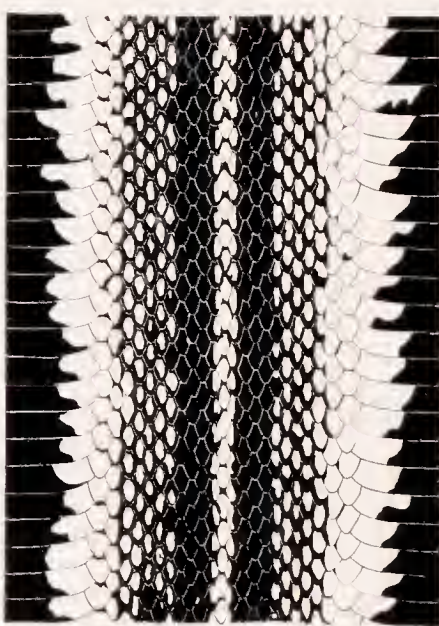
Fig. 3. MIXED
RINGED AND STRIPED

Fig. 4. BLACK VENTRUM

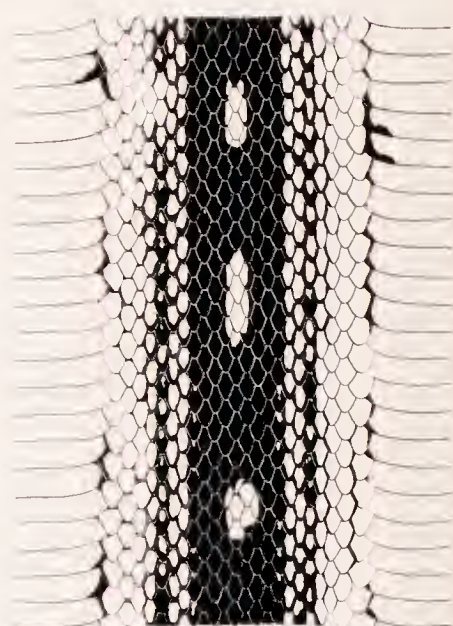


Fig. 5. BROKEN STRIPE

A FURTHER STUDY OF PATTERN DIMORPHISM IN THE CALIFORNIA KING SNAKE

INTRODUCTION

In a paper published in 1936 (*Herpetologica*, 1, 18-27), it was shown that the ringed and the longitudinally-striped king snakes of southern California, hitherto considered separate species, *Lampropeltis getulus boylii* and *L. californiae*, are in reality only pattern phases of a single species, *Lampropeltis getulus californiae*. This conclusion followed the hatching of two clutches of eggs, one laid by a striped, and one by a ringed mother. Each brood contained representatives of both pattern phases. More recently eight additional broods have been hatched. While these do not change the conclusions previously reached, they do provide some additional statistics on the inheritance and sex-linkage of these patterns, which seem to justify a supplemental report. However, before presenting the data on the newly available broods, it is necessary to develop certain statistics of the general king-snake population, especially sex- and pattern-ratios, in order to have a standard with which the broods may be compared.

This king snake does not possess the power to produce the dual pattern throughout its range, for the pure striped phase is found only in southern California and northern Lower California, in the region of which San Diego is the center, while the ringed phase has a much wider range. In the San Joaquin Valley of south-central California, and in the Cape region of Lower California, there is produced an occasional aberrant pattern, showing some similarity to the perfectly striped snakes of the San Diegan region; but these individuals are highly variable in nature and evidently represent a comparatively small proportion of the population. Elsewhere throughout the extensive range of the Pacific King Snake in southern Oregon, central and northern California, Nevada, Utah, and Arizona, only the ringed pattern has been found. Eastward to the Atlantic coast, other subspecies of *Lampropeltis getulus* occur, but all of these are ringed or spotted; none has developed an alternate striped phase.

PATTERN DIMORPHISM IN THE GENERAL POPULATION

There are indications that, even in San Diego County, the power to produce the striped pattern is not present to the same degree in the snakes on the desert side of the mountains. We have the following statistics of the frequency of occurrence of the two forms in the county, as derived from a 16-year record of the snakes reported from this area:

Area	Ringed	Striped	Per Cent Striped
Coast	511	357	41.1
Inland Valleys and Mesas.....	330	211	39.0
Coastal Foothills	160	137	46.1
Mountains	19	14	42.4
Subtotal	1,020	719	41.4
Desert Foothills	40	5	11.1
Desert	9	0	0.0
Total	1,069	724	40.4

Thus we find a fairly constant proportion of striped snakes eastward from the coast, in the zones to and including the mountains, with a conspicuous falling off on the desert slope. By the chi-square method of testing the significance of the difference between the proportions exemplified by two groups, we find that the ratios in the desert foothills and the desert are significantly different from those which obtain on the coastal side of the mountains. Thus, we conclude that the transmontane snakes do not possess the genetic factor which produces the pattern alternation to the same extent as their coastal congeners. The zonal ratios in the four zones, from the coast to the mountains inclusive, are found by test not significantly different from the general mean or from each other. Hence we consider 41.4 per cent striped (and mixed) snakes, the weighted mean in these four zones, to represent our best estimate of the composition of the coastal population, and this figure will be used in commenting on the ratios in the broods. For the purposes of this tabulation all specimens having a pattern mixture were classified as striped, since the statistics of these aberrant snakes were not kept with sufficient accuracy to permit separate groupings. The characteristics of these aberrant patterns will be subsequently discussed.

To give an idea of the consistency of the percentage of the striped phase out of the total cismontane population, we present the figures for the 16 successive years making up the total given in the previous table:

Year	Striped Snakes	Ringed Snakes	Total Snakes	Per Cent Striped
1923	32	52	84	38.1
1924	29	52	81	35.8
1925	44	59	103	42.7
1926	37	46	83	44.6
1927	55	55	110	50.0
1928	44	50	94	46.8
1929	41	70	111	36.9
1930	80	86	166	48.2
1931	35	57	92	38.0
1932	16	42	58	27.6
1933	33	63	96	34.4
1934	45	68	113	39.8
1935	55	94	149	36.9
1936	30	35	65	46.2
1937	65	78	143	45.4
1938	78	113	191	40.8
Total	719	1,020	1,739	41.4

It will be observed that the annual percentage of striped snakes varies from a maximum of 50.0 to a minimum of 27.6. No secular change in the ratio is evident; as a test, the totals for the first and last 8-year periods were compared and no significant difference was found in the proportions. No attempt should be made to attribute to a greater population the evident increase in the total number of snakes reported; the increase has resulted from certain conditions affecting the collecting and reporting of specimens rather than from any real change in the king snake population.

STANDARD PATTERNS

Although, from the statistics thus far presented, it might be presumed that these king snakes may be readily and consistently divided into two pattern groups, such is not the case; for there is a considerable variability in each of the two patterns, and this is further accentuated in a small proportion which seem to be mixtures or pattern intermediates. In order to clarify the discussion of these intermediates, it is necessary, first, to repeat the descriptions of the typical forms which appeared in the prior paper. These descriptions are particularly applicable to the San Diego County specimens, it being understood that the striped phase reaches its highest development in

this area, both in perfection of pattern and in numbers relative to the total population.

The ringed and striped phases do not differ essentially in head pattern; they are likewise similar in body color. The light marks in either may vary from white to buff, and the dark from red-brown through chocolate-brown almost to black. The color contrast is usually more accentuated in the young than in adults.

The ringed pattern consists of light cross-rings separated by dark, there being from 22 to 40 of these rings on the body and 6 to 10 on the tail (Fig. 1).^{*} The relative widths of the two sets of rings vary considerably; but usually the dark rings, where they cross the mid-dorsal line, are 3 or 4 times as wide as the light. Sometimes the light rings engage only a single scale, but more often they cover about 2 scales, end to end, where they cross the middle of the back. Laterally, as the light rings approach the ventrum, they widen at the expense of the dark, so that as they cross the belly the widths of the light and dark rings are approximately equal, or the light may be wider.

The striped phase has a light longitudinal stripe on the dark ground color from head to tail (Fig. 2). This stripe usually engages the mid-dorsal row and half of the row on either side, thus being two rows wide. The lateral edges of the stripe are generally even, but the stripe may be imperfect in a variety of ways; it may be broken into a series of dashes or spots; it may vary in width or be laterally offset in sections by a scale-row or two. Sometimes the edges are serrated. Breaks in the stripe on the tail are usual, the perfect stripe from head to tail-tip being rare indeed.

The lateral pattern is quite variable, but if we accept the specimens with the more perfect dorsal stripes as being those most truly representative of the striped pattern, we find the corresponding lateral pattern to consist of light lateral scale rows next the ventrals, with increasing darkness as the dorsum is approached. This gradual change is effected by a dark border around each scale, which border expands at the expense of the light center, continuously reducing the light spot. There is considerable variability in the row at which the light centers finally disappear from the scales, but this usually occurs from the 4th to the 8th row above the ventrals, thus leaving from $6\frac{1}{2}$ to $2\frac{1}{2}$ solidly dark rows on either side of the dorsal stripe.

Just as the mid-dorsal stripe is highly variable in quality, so also is the coloration of the lateral areas, which, deviating from what

^{*} While the figures show the light scales edged with dark, and vice versa, this is done to outline the scales. Actually the scales are unicolor.

seems to be the theoretical pattern, may be mottled, barred, or with longitudinal dashes in a variety of arrangements.

The belly of the striped phase is generally light, except that the outer edges of the ventrals are usually marked with dark blotches or irregular streaks. But it is highly characteristic of this pattern phase that the underside of the tail is always dark, there being no exception to this rule in more than 100 specimens investigated. The transition from light to dark occurs quite sharply at the vent or slightly posterior thereto.

ABERRANT PATTERNS

With a variability of this character and extent, particularly in the striped phase, it might be thought impossible to make any classification of those aberrant specimens in which the abnormal deviations of both are mixed; for the intermediates, even in those sections of the body which tend to follow one or the other pattern, often do not incorporate pure or typical patterns, but rather somewhat distorted analogues. For example, in the ringed sections of the intermediates the light rings are often narrower than is customary in the pure ringed phase, and do not widen laterally to the usual extent. And in the striped sections, the light dorsal line is likely to wander considerably from the expected mid-dorsal location.

Yet with all this variability we find it possible to divide the aberrants into three general groups, based on the predominance of three kinds of deviations from normal:

- (1) Snakes having both ringed and striped sections on the body (Fig. 3). Specimens with short cross-bars, which, however, do not cross the lateral scale rows just above the ventrals, are included in the third, rather than this group.
- (2) Snakes with dark ventrums (Fig. 4). In its most extreme form this type of aberrant has the belly all dark. A segregation has been made on the proportion of dark venter, specimens with more than half dark being allocated to this class.
- (3) Snakes with regularly interrupted mid-dorsal light lines (Fig. 5). In spite of the frequent irregularity of the dorsal stripe it is possible to segregate a particular group with this stripe rather consistently divided into a series of round light spots, or short longitudinal or cross dashes. Such an interruption on the tail alone is not considered significant, since nearly all specimens have this irregularity on the tail, even when the body stripe is unbroken. I have arbitrarily placed in this category such specimens as have at least 6 complete breaks in the mid-dorsal stripe on the body.

Before proceeding to the statistical data on these aberrants, I wish to mention some of their other peculiarities.

Mixed aberrants of the first type, which, by their very mixtures seem best to fit our ideas of what a true intermediate should be, have several peculiarities. Usually the striped sections are present at the head and tail, while the mid-body is ringed. Where the ringed part greatly predominates, the anterior striped section is likely to be suppressed, but the tail stripe persists. The light rings are often narrower than is usual in the pure ringed phase, and frequently they do not widen as they approach the ventrum, as in their pure analogues. In this these cross rings resemble the longitudinal stripes of the other pattern, turned sidewise. Thus these intermediates are generally darker than normal specimens.

Aberrants of the second group with dark ventrums are often heavily pigmented laterally as well. I have noted one specimen in which the lateral light scales are reduced to a single row above the ventrals. Sometimes the dark ventral color is concentrated on the outer edges of the ventrals, with a light streak down the mid-ventral line; but in other cases the opposite is true, with the dark streak or band in the middle. When a longitudinal color difference is evident, as is frequently the case, the dark pigment is concentrated posteriorly.

Aberrants of the third type are characterized by a considerable irregularity and are the least readily segregated of the three. The blotches, which represent a partly suppressed dorsal stripe, may be reduced to round rots, or they may be dashes, often twisted at an angle, or turned exactly crosswise. A black dorsum may go with this pattern, that is, a specimen may fall into both the second and third classifications.

There is a fourth, somewhat indefinite, group of aberrants which I have not sought to segregate from the striped specimens, since it is too difficult to assign definite limits for their classification. Their irregularities are largely evident laterally, although the mid-dorsal line is likely to be imperfect, with offsets and variations in width. On the sides there are light and dark bands of varying width, broken and separated by light and dark cross blotches, which do not, however, cross the dorsum. These specimens are few in number, some 5 or 6 out of three or four hundred. They resemble in some ways the aberrants which are found in the San Joaquin Valley; also, they are of frequent occurrence in the vicinity of Laguna Beach, Orange County. To some extent they also resemble the form from the Cape Region of Lower California which Van Denburgh described as *L. nitida*, but which I now consider a pattern-aberrant of the ringed

king snake of that region. In *nitida* there is much irregularity in both dorsal and side stripes and the ventrum is always dark. There is less contrast between light and dark areas than is the case in San Diego County; this characteristic is also observed in the aberrants of the San Joaquin Valley. Thus these snakes are dark mixtures of the other types of aberrants.

PROPORTION OF ABERRANTS

In preserving specimens for study, I made it a practice for a number of years to save all of those with peculiar patterns, while many of the more normal specimens were exchanged or exhibited at the zoo. This was a justifiable procedure from the standpoint of securing a maximum of aberrant material for study, but has had a distorting effect on the statistics gleaned from the composition of the collection. However, this artificial selection of aberrants was not effective in the case of the juveniles and hence the available young specimens may be taken as a sample of the normal distribution of patterns in this county.

Using such a segregation we have the following statistics on the specimens under 500 mm. in length, and presumably representing an unbiased sample of the San Diego County population:

Classification	Number	Per Cent of Total
Ringed	76	54.3
Striped	49	35.0
Aberrant		
Mixed Striped and Ringed.....	3	2.1
Black Ventrums	7	5.0
Broken Stripes	5	3.6
	140	100.0

It will be observed that the total percentage of aberrant specimens (10.7) considerably exceeds that given in the previous paper, wherein it was stated that the aberrants comprised about 3 per cent of the population. However, in the former paper only the mixed specimens having both patterns were recognized as aberrant.

It will be noted that in this sample the striped plus aberrant snakes comprise 45.7 per cent of the population as compared with the figure of 41.4 previously given for the population as reported from all sources. By test the difference is found to be without significance;

that is, there is no evidence that this is not a fair sample of the same population as that comprising the census.

SEXUAL DIMORPHISM

One other point remains to be discussed before applying these statistics to the broods, this being sexual dimorphism, and particularly whether there is any linkage between pattern and sex.

First as to the sex ratio in the population: all specimens available to me, not including the broods, have the following sex distribution:

	Males	Females	Total	Per Cent Males
Ringed Phase.....	88	90	178	49.4
Striped Phase*.....	76	61	137	55.5
Total	164	151	315	52.0

Testing these distributions by the usual chi-square method with the correction for continuity, we find that neither deviation is significantly different from a theoretical equality of the sexes; nor is there a significant difference between the sex ratios of the two patterns. We are therefore justified in concluding that the sexes occur in equal numbers among the king snakes, and that there is no sex-linkage with pattern, insofar as the two typical patterns are concerned.

But with the aberrant specimens we find a different situation, for a sex-linkage with pattern is evident. In this case we employ all available San Diego County specimens except the broods; since there was no conscious selection of these aberrant specimens with respect to sex, we are not restricted to specimens less than 500 mm. long. We have the following data:

Classification	Males	Females	Total	Per Cent Males
Mixed Pattern	16	1	17	94.1
Black Ventrums	2	12	14	14.3
Broken Stripes	5	11	16	31.3
Total	23	24	47	49.0

Testing these distributions against an assumed equal division of the sexes we find that the first two proportions are significantly different from a 50-50 sex ratio; that is, the observed discrepancies are not attributable to the chances of sampling. Broken stripes are, however,

* Including aberrants.

not definitely proven to be a sex-linked character ; in drawing sixteen individuals from a large population having a balanced sex distribution, there would be 21 chances in 100 of drawing 5 or less of one sex and 11 or more of the other.

Noting so few of one sex in two of the classes, one might suspect these particular individuals have been misplaced through inaccurate sexing. However, such is not the case ; while the sexing of juveniles is difficult, two of the individuals which break down what seemed at first to be a perfect correlation are adults, where no mistake could be made. For example, the single female in the first group, which had an unusually fine intermediate pattern, contained eggs.

It will be observed that if we take all of the aberrant specimens together, there seems to be no sexual unbalance. However, this is too small a sample to permit a dogmatic statement on this point.

BROOD DATA

Having derived from the available specimens such information as we may with respect to pattern- and sex-ratios, we now proceed to apply these statistics to the ten broods lately hatched, to see what may be learned concerning the inheritance of the patterns. Unfortunately we know nothing concerning the fathers of these broods, since all the pairs had mated in the wild before the mothers were caught. The pattern data on the broods are as follows :

		Pattern of Brood					
Brood Number	Mother	Normal		Aberrant			Total
		Ringed	Striped	Mixed	Dark Ventrums	Broken Stripes	
1935-2*	Ringed	2	1	..	..	1	4
1937-2	Ringed	4	..	..	..	..	4
1938-5	Ringed	7	..	..	..	..	7
1938-6	Ringed	9	..	..	..	..	9
1935-1*	Striped	..	1	1	3	1	6
1938-1	Striped	2	5	..	1	..	8
1938-3	Striped	1	1	..	1†	..	3
1938-4	Striped	..	4	..	2	..	6
1938-2	Dark Ventrums.	..	1	..	3	..	4
1937-1	Broken Stripes.	1	1	4	1	..	7
Total		26	14	5	11	2	58

* Reported in the previous paper. † Also has broken stripes.

The conclusions to be drawn from this table are:

- (1) A mother of either phase can produce pure patterned young of both phases, but
- (2) A mother tends to produce young of her own phase.
- (3) The proportion of intermediates and aberrant specimens, amongst these broods hatched in captivity, is greater than in the general king snake population of the county.

Conclusion (1) is self-evident from the statistics. No less than four of the broods contain individuals with pure patterns of both phases. One of the mothers was ringed, one an aberrant, and two were striped.

However, conclusion (1) does not by any means justify the corollary that the pattern of the progeny is independent of that of the mother. On the contrary, taking only the pure-patterned mothers and progeny, we have the following contingency table:

Mother	Brood		
	Striped	Ringed	Total
Striped	11	3	14
Ringed	1	22	23
Total	12	25	37

It requires no calculation to demonstrate that this distribution indicates a high correlation between the pattern of the mother and that of the progeny; there is a highly significant difference between the progeny of the two classes of mothers.

Another way of looking at the same situation is the following. It will be observed that three out of the ten broods have pure progeny of the same pattern as the mother. The possibility of this occurring by chance is exceedingly small. For example, take Brood 1938-5 (seven ringed young from a ringed mother) and assume a population ratio of 41.4 per cent striped and 58.6 per cent ringed. If pattern were purely a matter of chance, we apply a binominal distribution and find that only one brood in 42 having seven young would come out all ringed. Similarly, with nine young, only one brood in 123 would be all ringed. Yet we have both of these contingencies occurring in ten broods, besides another uniform brood of four snakes. Conclusion (2) is therefore inevitable: The patterns of the young are related to that of the mother—a mother tends to produce young of her own phase.

It is found from the above table that, neglecting aberrants (both mothers and offspring) striped mothers produce 78.6 per cent striped young, and 21.4 per cent ringed; while the ringed mothers produce 4.3 per cent striped young and 95.7 per cent ringed. These ratios are

not consistent with a general population proportion of 41.4 per cent striped, for, starting with these ratios, the proportion in the next generation would be only 35.1 per cent striped ($78.6 \times 41.4 + 4.3 \times 58.6$). We may therefore presume that if the two phases are equally prolific as regards sizes of broods, a greater number of broods than has been available to us would show a slightly higher production of striped young by either or both phases of mothers. For example, if striped mothers produced 80 per cent, and ringed mothers 14 per cent striped young, a population balance similar to that noted would be obtained. These ratios could be properly worked out if we had a larger series of broods and knew the patterns of the fathers.

The third conclusion, that the broods have a higher percentage of aberrant individuals, is evident from the following table:

	Normal	Aberrant	Total	Per Cent Aberrant
Available specimens				
under 500 mm.....	125	15	140	10.7
Broods	40	18	58	31.0

The higher proportion of aberrants in the broods is found to be statistically significant. However, this may be explained by the presence of the two aberrant mothers. It is obvious that they have produced more than their shares of the aberrants, since their broods contained only 3 normal snakes to 8 aberrants, or 73 per cent abnormal, compared to a population average of 10.7 per cent. Two aberrant mothers out of a total of 10 is a larger than average percentage of aberrant mothers than would be evident if more broods were available; one in nine would be similar to the proportion in the general population. Taking half of the young snakes in the two broods of the aberrant mothers, plus all broods from the normal mothers, we have the following contingency table:

	Typical	Aberrant	Total
Broods	38½	14	52½
General Population	125	15	140
Total	163½	29	192½

Using the chi-square method with correction for continuity, we find that there is only a little more than one chance in a hundred that this difference in proportionalities could occur by chance. We are therefore justified in the conclusion that these broods, hatched in

captivity have a higher proportion of aberrants than the general population.

It is evident that there is a greater tendency for the striped mothers to produce aberrant young than the ringed mothers, as indicated by the following table:

	Normal	Aberrant	Total	Per Cent Aberrant
Striped Mothers	14	9	23	39.1
Ringed Mothers	23	1	24	4.2
	—	—	—	—
Total	37	10	47	21.3

This difference is found to be significant. Also, the difference between the proportion of aberrant young produced by the striped mothers proves to be significantly higher than the proportion found in the general population, as represented by the young under 500 mm. But the small number produced by the ringed mothers is not significantly lower than that evident in the general population. The fact that aberrant mothers are fertile is also of interest.

Returning to the first conclusion respecting the high proportion of intermediates and aberrant specimens amongst broods hatched in captivity, we observe that if this ratio is greater than in the general population, such a peculiar situation might result from one of the three following conditions:

(a) Pattern aberrance in juveniles may be correlated with other characters of a lethal nature, so that many of these queer specimens do not long survive.

(b) The pattern, particularly the dark dorsum, may change with age.

(c) The captivity of the mothers may affect the progeny.

I think that *b* is ruled out by the fact that there is no indication of color changes in king snakes with age, except for a gradual lightening of the dark brown or black areas in the juveniles, to chocolate or medium brown in the adults. But at all times the pigmented areas may be easily distinguished from the unpigmented, and there is no evidence that either changes ontogenetically at the expense of the other. Full grown specimens with dark ventrums are occasionally found and it must be remembered that the underside of the tail is dark in all striped specimens. This would seem to leave the choice between *a* and *c*, with *a*, the suppression of aberrants by the presence of lethal or harmful characters, as much the more likely. I have previously mentioned a similar high percentage of aberrant and defective young

amongst rattlers born in captivity. It would be rather fantastic to suppose that captivity could affect the patterns of the young snakes.

As nothing is known concerning the fathers of these broods, we can make no useful deductions with regard to a law of pattern inheritance. The percentage of striped snakes is found to be significantly above the ratio for a simple mendelian recessive.

SEX-PATTERN LINKAGE IN BROODS

The sex distribution amongst the broods was as follows:

	Normal		Aberrant			Total
	Ringed	Striped	Mixed	Dark Ventrums	Broken Stripes	
Males	15	8	5	2	2	32
Females	11	6	0	9	0	26
Total	26	14	5	11	2	58
Percent Males	57.7	57.1	100	18.2	100	55.1

The decided sexual unbalance amongst the aberrant specimens continues in evidence. Combining these broods with our previous tabulation of the aberrants from the general population, we have:

Classification	Males	Females	Total	Per cent Males
Mixed pattern	21	1	22	95.5
Black ventrums	4	21	25	16.0
Broken stripes	7	11	18	38.9
Total	32	33	65	49.2

The mixed pattern and black ventrums are significantly sex-linked; this is not true of the broken stripe pattern. Evidently, aberrance in males is usually accompanied by a mixed or intermediate dorsum, while in females it is evidenced by a dark ventrum; no doubt these two patterns are sexually complementary.

INDEPENDENCE OF PATTERN AND LEPIDOSIS

In the previous paper (p. 21) it was shown that there are no scale-count differences which are correlated with the pattern dimorphism, that is to say the ringed and striped phases have scale counts differing insignificantly in means and dispersions. With the added specimens now available this conclusion remains unchanged; we find no signifi-

cant differences in scale rows, ventrals, caudals, supralabials, or infralabials. These conclusions are based on 167 of the ringed and 103 of the pure striped phase, all from San Diego County, with the broods excluded. We do find, rather unexpectedly, that there is sexual dimorphism in dorsal scale rows, the female snakes averaging slightly higher than the males. In our subsequent calculations we have treated the sexes separately in dealing with scale rows, just as we do with ventrals and caudals, in which sexual dimorphism is so obvious as to require no calculation for its demonstration.

Having found no differences in lepidosis between the ringed and striped specimens, we pool their scale counts to secure a larger sample of the parent population. With this as a basis of comparison we make two investigations to determine: (1) whether specimens aberrant in pattern are in any way peculiar in scale counts as well; and (2) whether the broods differ significantly in scale counts from the general population.

The answer to the first question is in the negative: Specimens aberrant in pattern are not significantly different in any character of lepidosis from the rest of the population. Thus this queer manifestation of pattern dimorphism carries with it no differences in scalation, either with respect to the two pure pattern phases, or the aberrants which are mixtures of the two.

In the case of the broods there are certain differences which do approach the level of significance, but it would probably be well to reserve a final opinion on this point until a greater number of broods becomes available. There are indications both of the inheritance of atypical scale counts and arrangements; and also of the presence amongst the broods of variants from the mode so unusual as to lead to one of the hypotheses previously mentioned—either that these abnormalities are the result of captivity on the mother, or, much more probably, they are linked with lethal characters, so that the young which carry them do not survive.

As examples of the inheritance of peculiarities the following may be cited: One mother has the fourth infralabials on both sides of the head divided in a peculiar way; two out of her brood of eight show the same peculiarity, but on the left side of the head only. Another mother with ten infralabials has a higher than normal number of young with this number of infralabials. Yet this type of inheritance is not always evident, since a mother with a divided mental did not produce any young with this characteristic.

As to the other type of peculiarity, we find amongst the broods a surprisingly high proportion without loreals, the loreal being fused

either to a prefrontal, postnasal, or preocular. Also a number have an upper postocular fused to the supraocular. One specimen (a female) has only 41 subcaudals, the lowest of 155 specimens. This is 4 less than the next lowest, and is 3.7 standard deviations below the mean (52). This is similar to some of the radical deviations observed amongst rattlesnake broods.

PERIOD OF INCUBATION

The eggs were laid between June 23rd and August 2nd, and hatched between September 5th and October 10th. The period of incubation varied between 71 and 86 days, the average being 76.

Batches of eggs were kept on slightly moistened paper in small individual crocks with a glass plate as a cover. This method, devised by C. B. Perkins, is proving highly successful in hatching the eggs of many species.

LIMITATIONS OF PATTERN DIMORPHISM

Viewed broadly the most interesting feature of this case of pattern dimorphism is its territorial limitation, compared to the range of the subspecies as a whole; and the peculiar modifications which occur on the periphery of the affected area. These modifications entail a reduction in the frequency of occurrence of the atypical form and coincidentally a change in the manifestation of that form.

First we have the situation in western San Diego County. Here, in a small area hardly greater than 50 by 50 miles, the longitudinally striped phase, so different from the ringed snakes which characterize the genus, number about 32 per cent of the population. An additional 10 per cent are intermediates between the ringed and the striped forms, or are modifications more closely resembling the latter. Thus 42 per cent of the population are atypical.

As we go out from this center we find a decreasing proportion of atypical specimens. Unfortunately the statistics from outside the county are meagre. From Chino, San Bernardino County, California, out of some fifteen specimens only one was aberrant. In Los Angeles County, the striped form is present, but reduced in relative numbers. Eastward from San Diego, on the desert slope, I have already shown (p. 6) that the production of the atypical form is significantly lower in proportion than on the coast. Likewise to the south the striped form is rarer, although it is known to occur at least as far south as Ensenada. At San Jose (Lat. 31°) in Lower California seven king snakes were collected and all were ringed; persons living in that vicinity when shown striped specimens said they had never seen such a snake thereabouts.

Coincidentally while the striped phase decreases in numbers with the distance from San Diego, the deviations of the atypical specimens from the pure striped pattern increase. Thus such atypical snakes as are found more nearly resemble those which have been termed aberrants in San Diego County. Although I have seen pure striped specimens from ten miles north of Ensenada, Lower California, the aberrants comprise a majority of those which are not ringed; in fact, the prevalence of mixed, rather than pure striped specimens, is already noticeable at Tijuana on the U. S.-Lower California border.

To the north pure striped snakes have been seen at Temecula, and are said to occur in the vicinity of Hemet, Riverside County. Along the coast I have no definite records of the pure striped pattern from any point north of San Diego County. Although atypical specimens are not uncommon at San Clemente and Laguna Beach, in Orange County, and at various points in Los Angeles County, they are all of patterns, which, in San Diego County, would be termed aberrants—none has yet been collected with a clear and even mid-dorsal stripe. Further to the north, in the San Joaquin Valley, the atypical specimens are still rarer, and the patterns more broken and imperfect. The same is true at the southern limit of pattern dimorphism, in the Cape region of Lower California, where the form described by Van Denburgh as *L. nitida* may, by analogy, be assumed to be an aberrant phase of the ringed snakes of that vicinity. Some of the San Joaquin Valley snakes closely resemble these Cape specimens.

In talking over this situation, Dr. Jean Linsdale has suggested that the power to produce striped and aberrant pattern phases might well be recognized as a subspecific character. From a nomenclatorial standpoint, there is much to recommend this, since there is now no way to distinguish between the snakes of Utah (for example) where all are ringed and those of southern California. Under such a scheme, if we include in *californiae* all snakes which have the power to produce an atypical pattern, even though it may not be the pure striped phase, we would place in the subspecies *Lampropeltis getulus californiae*, the king snakes inhabiting the southern San Joaquin Valley, southern California, and Lower California. Elsewhere in California, and in Oregon, Nevada, Utah, and western Arizona, the snakes of this form would be referred to as *Lampropeltis getulus boylii*, a more desirable and appropriate name, since this was the name by which they were long known, prior to the discovery that *californiae* was only a pattern phase of the ringed snake, rather than a separate species. This allocation of names would involve no violation of the Code, provided the power of pattern dimorphism be accepted as a

valid subspecific character. The only objection is the necessity for classifying newly acquired ringed specimens on purely geographical criteria, depending on whether striped or aberrant snakes are known to occur in the same territory.

In the southwest there are three other pairs of snakes, now recognized as separate species, which may later prove to be pattern phases. They are:

Coluber flagellum frenatum and *C. piccus*

Phyllorhynchus decurtatus decurtatus and *P. browni*

Sonora semiannulata and *S. miniata*.

The first is more a case of color, than pattern dimorphism—a color difference somewhat like melanism, yet not true melanism, since the ventral surfaces are unaffected. Intermediates are found and it is thought that broods will eventually prove these forms identical. One of the peculiarities of the king snake situation is in evidence, namely, *C. piccus* is found in only a small part of the range covered by *C. f. frenatum*.

Of the leaf-nosed snakes, no intermediates between *P. d. decurtatus* and *P. browni* have yet come to light. The only indication that they may be pattern phases, rather than separate species, is a parallel territorial trend in lepidosis.

The ground snakes also are in an uncertain category because of lack of adequate material. They show certain parallel tendencies which may indicate a case of pattern dimorphism; for example, both forms from Boulder City, Nevada, are peculiarly spotted on the sides.

It is to be hoped that the availability of broods may in the future solve these problems as they have that of the king snakes.

ACKNOWLEDGMENTS

I have been assisted in this investigation by Mrs. Elizabeth Leslie, who made many of the statistical computations; and by L. H. Cook, Charles Shaw, James Deuel, and Morris Bloomfield, who made scale counts. The first two broods were hatched at the San Diego Zoo by Robert S. Hoard, the others by C. B. Perkins. The figures were prepared by Norman Bilderback. Harold Woodall has kindly supplied data on Los Angeles County specimens. To all I am grateful.

SUMMARY AND CONCLUSIONS

A further investigation of the peculiar pattern dimorphism evident amongst the king snakes of the San Diegan region of southern Cali-

fornia belonging to the subspecies *Lampropeltis getulus californiae* indicates that five pattern types are in evidence. Two of these comprise about 90 per cent of the population. The other three are intermediates, two of them being sex-linked. A mother of any phase can produce young of any other phase, but tends to produce a high proportion of young of her own phase. Broods hatched in captivity are found to have a higher percentage of aberrants than the general population, indicating a probable high mortality amongst aberrants. Pattern phases are not correlated with differences in lepidosis.

The power to produce the major pattern variant is restricted to a relatively small area within the range of the subspecies. On the periphery of this area the atypical specimens are reduced in number and are imperfect in the nature of their deviations, somewhat resembling a small proportion of mixed specimens in the central area. Beyond this periphery there is a much larger area inhabited by the same subspecies but in which there seems to be no power to produce any of the atypical patterns.

NOTE.—While this paper was in press the 1939 broods hatched. Using the classification set forth in tabular form on p. 13 the results were as follows:

Brood Number	Mother	Pattern of Brood					Total
		Normal		Aberrant			
				Mixed	Dark	Broken	
		Ringed	Striped		Ventrums	Stripes	
1939-1	Ringed	2	1	..	1	..	4
1939-2	Striped	2	5	..	..	..	7
1939-3	Striped	2	7	..	1	..	10
Total		6	13	0	2	0	21

These additional broods do not modify any of the conclusions previously reached. Once more mothers of each phase produced perfect young of both phases.



Fig. 6. CONTRAST OF DORSAL PATTERNS
Ringed phase at the left; Striped phase at the right.

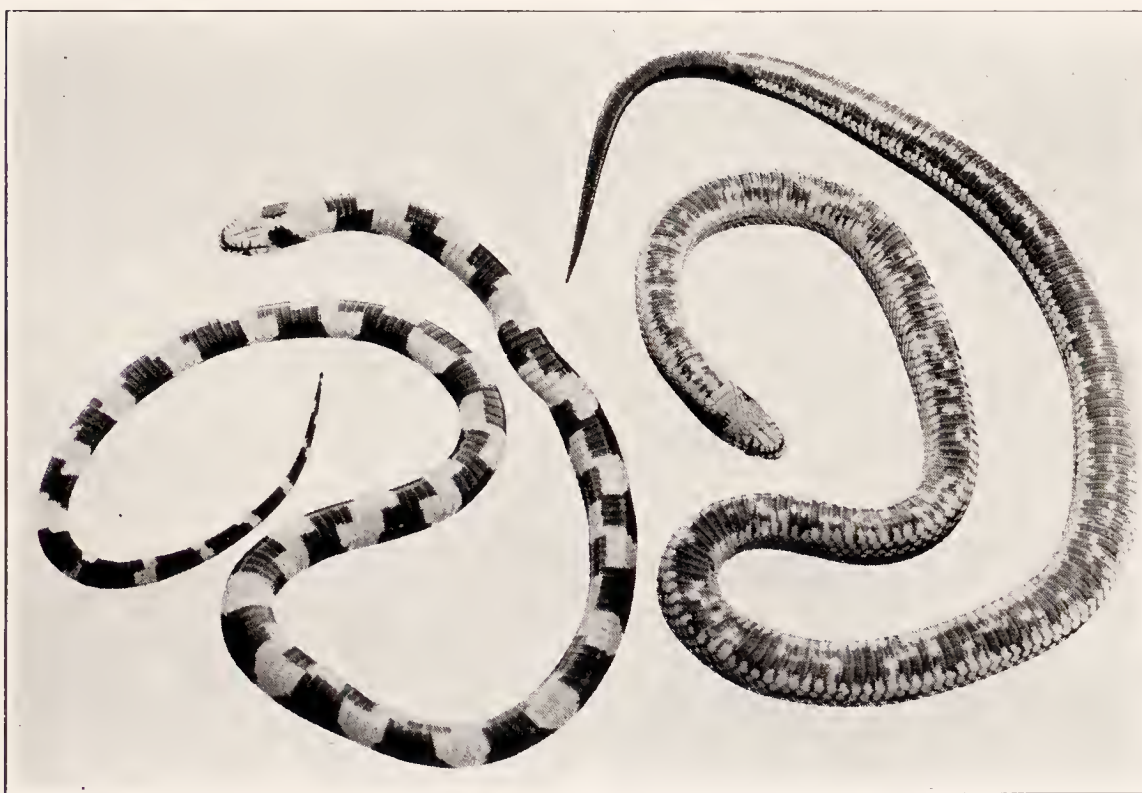


Fig. 7. CONTRAST OF VENTRAL PATTERNS
Ringed phase at the left; black ventrum at the right.
(Photographs of anesthetized specimens from
San Diego County, California)

